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Abrachium, a new genus in the *Clathraceae*, and *Itajahya* reassessed

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Abstract — Molecular and morphological analyses have elucidated phylogenetic relationships of two remarkable species in the *Phallales*: *Aseroe floriformis* and *Phallus roseus*. Genes from ATPase subunit 6 (atp6), the nuclear large subunit ribosomal DNA (nuc-LSU), and the second largest RNA polymerase II subunit (RPB2) underwent Bayesian and parsimony molecular analyses. Molecular datasets, combined with morphological characters, support a new genus (*Abrachium* for *Aseroe floriformis*), reassessment of *Itajahya,* and emendation of *Clathraceae*.

Key words — *Phallomycetidae*, gasteroid fungi, neotropics, phylogeny, evolution

Introduction

Fischer (1898-99) established the order *Phallales*, initially composed of two families, *Clathraceae* and *Phallaceae*, to separate representatives with branched and unbranched basidiomata. *Clathraceae,* established by Chevallier (1826), encompasses the "lattice stinkhorns", fungi that exhibit a peculiar basidioma featuring tubular or mucilaginous arms either interconnected or intertwined in a network or comprising a receptacle with vertical arms either connected at the top or arched in the shape of a star (Miller & Miller 1988). Pegler & Gomez (1994) included twelve genera within the family (*Blumenavia, Linderiella, Pseudocolus, Anthurus, Aseroe, Lysurus, Clathrus, Ileodictyon, Simblum, Colus, Neolysurus* and *Kalchbrennera*).

Corda (1842) proposed *Phallaceae* for species with fruiting bodies composed of a single, hollow receptacle with a foul-smelling gleba covering the apex. Morphological characters widely used to separate genera include

the presence of a campanula (head) at the apex of the receptacle in *Phallus*, indusium in *Dictyophora,* and calyptra in *Itajahya*. Some genera lack a distinct head and form the mucilaginous gleba directly on the apical receptacle (e.g., *Mutinus*) or at a constriction near the apex (e.g., *Staheliomyces*). Several attempts were made to establish a synopsis of the family (Lloyd 1909, Fischer 1933), and Cunningham (1944) included seven genera: *Dictyophora, Itajahya, Phallus, Mutinus, Staheliomyces, Aporophallus,* and *Floccomutinus.* However, Kreisel (1996) viewed *Dictyophora, Aporophallus, Itajahya, Echinophallus,* and *Endophallus* as subgenera of *Phallus* sensu lato, using the shape and surface of the head, pigmentation of the receptacle, and morphology of the volva and rhizomorphs as primary characteristics. He did not deem the presence of a pore at the receptacle apex or the morphology of the head, indusium, and calyptra as sufficient for segregation at the generic level (Kreisel 1996).

Taxonomic studies of Neotropical phalloid species have revealed new and intriguing species (Baseia et al. 2003, Baseia & Calonge 2005, Fazolino et al. 2010). The discovery of new species is essential to understanding the evolutionary path of *Phallales* clades, since according to known estimates (Hawksworth 2001, Mueller et al. 2007, Blackwell 2011), most tropical species remain unknown. Through morphological data and molecular tools the classification of macrofungi should change in coming years.

The present study aims to evaluate the actual taxonomic position of *Aseroe floriformis* and *Phallus roseus*, two species with distinct morphological features that have not yet been analyzed by molecular studies.

Materials & methods

Basidioma sampling

Basidiomata were sampled at the Parque Estadual Dunas do Natal (06°22′10″ S and 35°00′28″ W) and Estação Ecológica do Seridó (06°35′02″ S and 37°17′02″ W), Rio Grande do Norte state, Brazil. Specimens of *Aseroe floriformis* and *Phallus roseus* were photographed and collected during the rainy seasons in 2008 and 2009. Materials studied were deposited in the fungal collection of the UFRN Herbarium.

Macroscopic characters were described from fresh specimens. Basidiomata colors were based on Kornerup & Wanscher (1978). Microscopic characteristics were determined from temporary mounts, hand-sectioned with a razor blade on the vertical axis of the basidiomata and mounted in 3% KOH and 1% cotton-blue lactophenol, respectively. All measurements were made under oil-immersion microscope objective at 1000× magnification. Spore measurements included the largest and smallest spores and at least 20 additional randomly selected spores from each specimen.

Molecular techniques

Fresh basidiomata of *Aseroe floriformis* (UFRN 1481) and *Phallus roseus* (UFRN 535) were used for CTAB DNA extraction. The CTAB buffer (1.4M NaCl, 100mM Tris-HCl pH 8.20mM EDTA and 2% CTAB) was added to 0.8g of fresh tissue pulverized

with liquid nitrogen and incubated for 30 min. at 65°C. After incubation, a chloroform-isoamyl (24:1) extraction was performed, followed by isopropanol precipitation. Total DNA amount was quantified on a NanoDrop-2000 spectrophotometer (NanoDrop Technologies Inc. Wilmington, DE 1980, United States).

DNA sequences were obtained for three different regions: nuc-LSU-rDNA (LROR/LR5), ATPase subunit 6 (ATP61/ATP62) and the second largest subunit of RNA polymerase RPB2 (bRPB2-6F/bRPB2-7R), with previously designed primers (Vilgalys 1990; Liu et al. 1999; Kretzer & Bruns 1999).

All PCR reactions were carried out in a final volume of 50µl, with PCR buffer 10X, 4 mM of $MgCl_2$, 25 ng of DNA, 0.3 mM of dNTP Mix, 12.5 pmol of each primer and 0.3µl of Invitrogen® DNA Taq Polymerase (5U/µl). The initial cycling parameter for atp6 reaction condition consisted of 2 min at 95°C for initial denaturation, 5 cycles of 35 s at 94°C, 55 s at 37°C and 1min at 72°C. This was followed by 30 cycles of 35 s at 94°C, 55 s at 45°C, 1 min at 72°C, and final extension of 5 min at 72°C with final hold of 4°C. The nuc-LSU-rDNA amplification condition underwent initial denaturation for 2 min at 95°C, followed by 39 cycles for 1 min at 94°C, 30 s annealing at 45°C, 1 min extension at 72°C, and a final extension for 5min at 72°C. RPB2 amplifications followed conditions described by Liu et al. (1999).

Amplicons were verified by ethidium bromide-stained 0.4% agarose gel electrophoresis. Total amount of amplified DNA was quantified by a NanoDrop-2000 spectrophotometer. Amplifications with low DNA content were re-amplified by increasing PCR cycles.

PCR products were purified with Wizard® SV Gel and PCR Clean-Up System (Promega). The sequencing reaction was performed with a DNA sequencing kit (BigDye® Terminator v3.1 Cycle Sequencing Kit) using the same primers employed to amplify each fragment, and sequencing was conducted an ABI 3730 DNA Analyzer (Applied Biosystems). Both were carried out at the Center for Human Genome Studies (University of São Paulo, CEGH-USP) and later assembled using DNA Baser v3.0.12 beta.

Phylogenetic analysis

Phylogenetic analyses were performed for three combined DNA datasets under Bayesian and parsimony criteria. Newly generated sequences for *Aseroe floriformis* and *Phallus roseus* ATP6, nuc-LSU-rDNA and RPB2 and those retrieved from GenBank (National Center for Biotechnology Information, http://www.ncbi.nlm.nih.gov – Table 1) were separately aligned using ClustalX2 (Larkin et al. 2007), with default settings (alignment files are available at http://purl.org/phylo/treebase/phylows/study/TB2:S11546). Manual adjustments were made in BioEdit v. 7.0.9.0 (Hall 1999). The three alignments were then concatenated with Phyutility (Smith & Dunn 2008). Maximum parsimony analyses were conducted with combined dataset file, in PAUP* (Phylogenetic Analysis Using Parsimony) version 4b10 (Swofford, 2002). Heuristic search was used with tree bisection-reconnection (TBR) and MULTrees. Confidence levels were established through 1000 bootstrap replicates. Bayesian analysis was carried out with combined dataset in MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001). Two different runs with four incrementally heated simultaneous Monte Carlo Markov chains were conducted over 2 million generations, applying respective substitution models determined for

each partition in MrModeltest v.2.2 (http://www.abc.se/~nylander/). Trees were sampled every 100 generations to produce 20,000 trees. In order to estimate posterior probabilities, 25% of the trees were discarded as a burn-in stage, observing when average standard deviation of split frequency (ASDSF) values dropped below 0.01.

Table 1. GenBank accession numbers used for phylogenetic analysis.

Species	GenBank Accession Number		
	nucLSU	ATP6	RPB2
Anthurus archeri	DQ218624	DQ218913	DQ219081
Abrachium floriforme	JF968440	JF968438	JF968442
Aseroe rubra	DQ218625	DQ218914	DQ219082
Clathrus chrysomycelinus	DQ218626	DQ218915	DQ219083
Claustula fischeri K.M. Curtis	—	—	DQ219086
Dictyophora duplicata (Bosc) E. Fisch.	DQ218481	DQ218765	DQ219087
D. indusiata (Vent.) Desv.	DQ218627	DQ218917	DQ219088
D. multicolor Berk. & Broome	DQ218628	DQ218918	DQ219089
Gelopellis sp.	DQ218630	DQ218919	DQ219090
Gelopellis sp.	DQ218631	DQ218920	DQ219091
Ileodictyon cibarium	DQ218633	DQ218922	DQ219093
I. gracile	DQ218636	DQ218925	DQ219096
Itajahya rosea	JF968441	JF968439	—
Kobayasia nipponica (Kobayasi) S. Imai & A. Kawam.	DQ218638	DQ218926	DQ219098
Laternea triscapa	DQ218640	DQ218928	DQ219099
Lysurus borealis (Burt) Henn.	DQ218641	DQ218929	DQ219100
L. mokusin (L.) Fr.	DQ218507	DQ218791	DQ219101
Mutinus elegans (Mont.) E. Fisch.	AY574643	AY574785	DQ219102
**Phallobata alba* G. Cunn.	DQ218642	DQ218930	DQ219103
**Phallus costatus* (Penz.) Lloyd	DQ218513	DQ218797	DQ219104
P. hadriani Vent.	DQ218514	DQ218798	DQ219044
P. ravenelii Berk. & M.A. Curtis	DQ218515	DQ218799	DQ219105
Protubera borealis S. Imai	DQ218516	DQ218800	DQ219106
P. canescens	DQ218645	DQ218932	DQ219108
P. jamaicensis (Murrill) Zeller	DQ218647	DQ218933	DQ219110
P. maracuja Möller	DQ218518	DQ218802	DQ219111
P. parvispora Castellano & Beever	DQ218648	DQ218934	DQ219112
P. sabulonensis Malloch	DQ218649	DQ218935	DQ219113
Simblum sphaerocephalum Schltdl.	DQ218521	DQ218806	DQ219115
**Trappea darkeri* (Zeller) Castellano	DQ218651	DQ218938	DQ219116
Pseudocolus fusiformis	AF213128	—	—

* Species used as outgroup

Results

Phylogenetics analysis

Bayesian and maximum parsimony analyses produced no significant differences in tree topology, indicating data consistency to resolve the phylogeny of the group. The phylogram (Fig. 3) illustrates six well-formed clades corresponding to the families of *Phallales* with high support values (PP = 1, BT = 90–100). Intergeneric relationships in each family are also shown. It was found that *Aseroe floriformis* does not cluster with *Aseroe rubra*, and occupies a basal position in the *Clathraceae*, with PP = 1 and BT = 99. In *Phallaceae*, *Phallus roseus* occupies a position between *Mutinus elegans* and other *Phallus* species, including indusiate representatives (*Dictyophora*), which cluster into a single clade displaying high levels of reliability (PP = 1, BT = 94).

Taxonomic revision

Based on the morphological and molecular data set, we propose a new genus to accommodate *Aseroe floriformis*. The most important morphological feature of the new genus —the lack of arms— requires an emendation in *Clathraceae*. Phylogenetic analyses also support the status change of the genus *Itajahya* in *Phallaceae*.

Clathraceae Chevall. **emend.** Baseia

Emended description: Basidiomata sessile to shortly stalked, upright receptacle, spreading, sometimes arched and united arms or a latticed receptaculum composed of interconnected tubular or gelatinous arms expanding from a flaccid button, which acts as a volva, or armless sunflower-shaped receptacle. Gleba located on the central disc of receptacle or inside and next to the clathrate receptaculum. Peridium three-layered. Basidiospores narrowly elliptical, covered with mucilaginous layer.

Type genus: *Clathrus* P. Micheli ex L.

Other genera: *Abrachium* Baseia & T.S. Cabral, *Aseroe* Labill., *Blumenavia* Möller, *Pseudocolus* Lloyd, *Lysurus* Fr., *Ileodictyon* Tul. & C. Tul.

The genus *Aseroe* was proposed by Labillardière (1800), with *Aseroe rubra* Labill. as the type (and only) species. Fischer (1890) subsequently described *A. arachnoidea.* Yoshimi & Hongo (1989) added *A. coccinea*, a name recently validated by Kasuya (2007). Baseia & Calonge (2005) discovered a new species, *Aseroe floriformis*, in northeastern Brazil in sand dunes. Although Index Fungorum lists 27 names in *Aseroe*, the latest edition of the Dictionary of Fungi (Kirk et al. 2008) lists only two: *A. floriformis* and *A. rubra*. The genus has a pantropical distribution, although *A. rubra* has been reported in Europe (Spooner 2005). *Aseroe* is characterized by a cylindrical receptacle and stipe

that emerge from a whitish volva. With the exception of *Aseroe floriformis*, all species have apical free arms internally covered by the gleba (Dring 1980).

Abrachium Baseia & T.S. Cabral, **gen. nov**.

MycoBank MB 561618

Ovo subglobosae, epigaeo, rhizomorphis basalis. Stipite cylindrico, spongioso. Receptaculum floriformis cum disco sine ramulis, centralis perforatae cum gleba gelatinosa marginata, foetida. Sporis cylindraceo-bacilliformis, laevis, hyalinae.

Type species: *Abrachium floriforme* (Baseia & Calonge) Baseia & T.S. Cabral

Etymology: *Abrachium*, due to the absence of arms.

Key characters: Egg subglobose, epigeous with several and basal mycelial cords, white. Stipe cylindrical, spongy. Receptacle with the same anatomy, sunflower-shaped, without arms, central disc covered by a gelatinous gleba. Spores cylindrical to bacilloid, smooth, hyaline.

Abrachium floriforme (Baseia & Calonge) Baseia & T.S. Cabral, **comb. nov**. Fig 1

MycoBank MB 561619

≡ *Aseroe floriformis* Baseia & Calonge, Mycotaxon 92: 170, 2005.

Specimens examined: **BRAZIL**, **Rio Grande do Norte**, Natal, Parque das Dunas, ad solum arenarius, 3-VII-2004, legit I.G. Baseia & P.P.T. Lacerda, UFRN-Fungi 1851 (holotype); 07-V-2009, legit I.G. Baseia UFRN 1481, GenBank JF968440, JF968438, JF968442.

Our phylogenetic analyses confirm high support values for *Phallales* in accordance with Hosaka et al. (2007). Morphological and molecular analyses supported the establishment of the genus *Abrachium*, named for its armless receptacle (Fig 1). This taxon was originally described in the Brazilian Atlantic rainforest (Baseia & Calonge 2005), but has since been recorded in northeastern Brazil (Trierveiler-Pereira & Baseia 2009, 2011, Bezerra et al. 2009).

The clathraceous clade comprises members with a variable morphology of the basidiomata, consisting of tubular or gelatinous arms either interconnected or free (Dring 1980). The armless receptacle of *Abrachium* justifies an emendation in *Clathraceae* and seems to be a primitive characteristic of the clade, as shown in the tree obtained by molecular inference (Fig. 3). Molecular data indicate that receptacle morphology is a phylogenetically informative characteristic in *Clathraceae*. In phylogram, *Abrachium* represents a basal clade, which is a sister group of a clade formed by other *Clathraceae* species. The latter have a bifurcation leading to two other subgroups. The first subgroup either has arms attached at the ends [*Pseudocolus fusiformis* (E. Fisch.) Lloyd], or free and arched like a star [*Aseroe rubra* and *Anthurus archeri* (Berk.) E. Fisch.]. The second subgroup displays a complex structure, forming a "cage" type configuration including *Clathrus chrysomycelinus* Möller, *Laternea triscapa* Turpin, *Ileodictyon cibarium* Tul. & C. Tul., *Ileodictyon gracile* Berk.,

Figures 1–2. Fresh specimens: 1. *Abrachium floriforme*. 2. *Itajahya rosea*. Bar = 10 mm.

and *Protubera canescens* G. W. Beaton & Malajczuk. Based on these data, we can infer that the evolution to receptacle bifurcation (forming arms, e.g., *Aseroe*) occurred at least once in the Neotropical region. Presumably, after the divergence of *A. floriforme*, a common ancestor has diverged to forms where the receptacle may bifurcate like arms in one group, and form a cage in the other (such as *Ileodictyon*).

Itajahya rosea (Delile) E. Fisch., Ber. Deutsch. Bot. Ges. 47: 294, 1929. Fig. 2

≡ *Phallus roseus* Delile, Flore d'Égypte: 300, 1813.

Specimen examined: **Brazil**, **Rio Grande do Norte**, Serra Negra do Norte, Estação Ecológica do Seridó, ad solum arenarius, 23-V-2008, legit T.B.S. Ottoni, UFRN-Fungi 535; GenBank JF968441, JF968439.

Molecular data analysis of *Phallus roseus* points to the need for reassessing its current taxonomic status in the subgenus *Itajahya* proposed by Malençon (1984) and Kreisel (1996). *Itajahya* was established by Möller (1895) based on *I. galericulata* Möller, a taxon discovered in Santa Catarina state, Brazil. The main feature distinguishing *Itajahya* from other *Phallaceae* genera is the presence of a structure called a calyptra (Fig. 2) located at the apex of the gleba (Möller 1895, Malençon 1953, Ottoni et al. 2010). Molecular data demonstrated that *P. roseus* diverged after *Mutinus* and prior to other species of *Phallus* (Fig. 3). Since *I. rosea* does not cluster with any other *Phallus* species, we propose

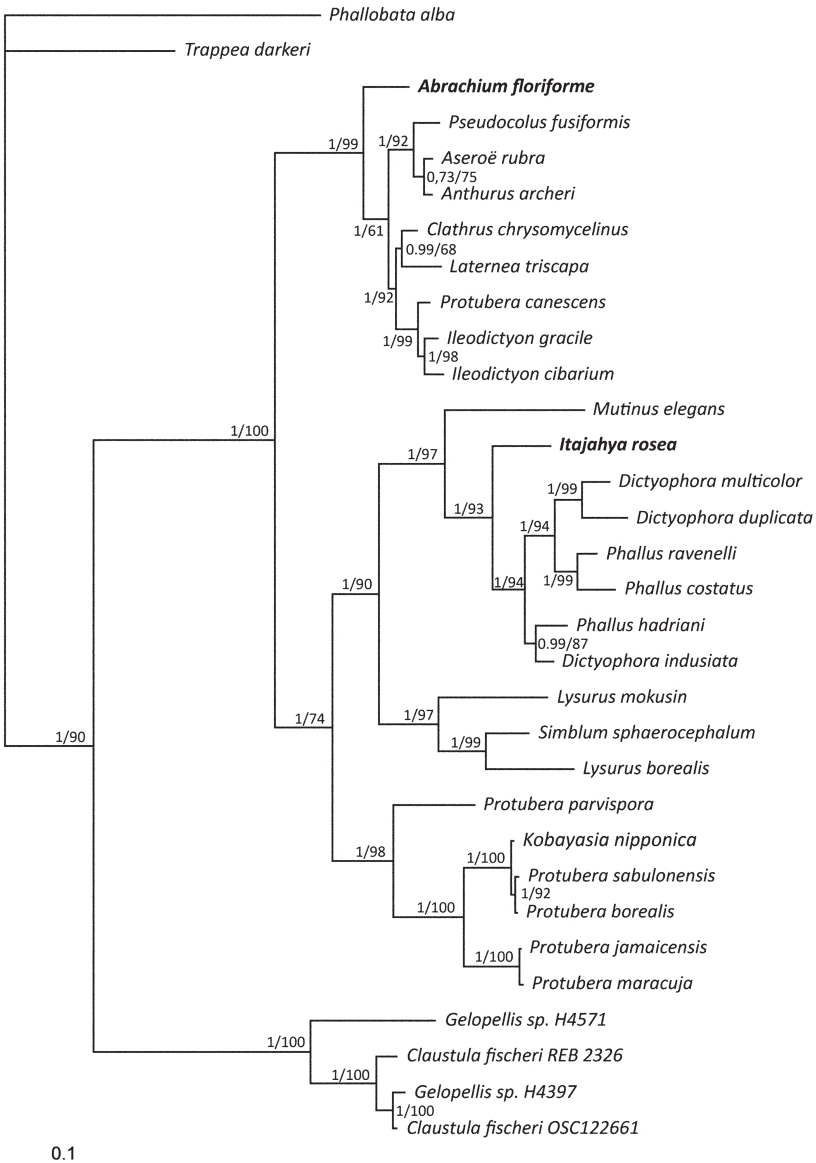

Figure 3. Phylogenetic tree of *Phallales* obtained through Bayesian analysis of atp6, nuc-LSU rRNA, and RPB2 sequences. Numbers preceding '/' = Bayesian posterior probability values (PP) and after '/' = maximum parsimony bootstrap values (BT).

raising *Itajahya* to generic status. Further collections and molecular studies of *I. galericulata* (= *Phallus galericulatus* (Möller) Kreisel) are also needed in order to ensure morphological characteristics (mainly the presence of calyptra) agree with molecular data recognizing the genus *Itajahya*.

Molecular data also imply that the indusium is not a phylogenetically informative character in *Phallaceae*. Malençon (1984) and Kreisel (1996) stated that species may be closely related with or without this structure, and that a species may or may not produce it or have a rudimentary form of it. The phylogram indicates that although *Dictyophora multicolor* and *D. duplicata* form a separate clade, *D. indusiata* clusters with *Phallus hadriani*, exhibiting prior divergence with the other mentioned clade. This suggests that indusiate species may have emerged independently during several phases of the group's evolution, thereby characterizing it as a polyphyletic assemblage. The phylogram also illustrates that *Mutinus* is a more primitive genus in *Phallaceae*, as observed by Cunningham (1944), based on data from simple sporophore morphology and the absence of complex structures such as campanulate apex, indusium and calyptra. It is important to note that further molecular studies are needed, especially with key-taxa that may lead to a change in current classification and give us a clearer picture of the systematics and evolution of phalloid fungi.

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